XXIII.—*A few Remarks on* Dipterus *and* Ctenodus, *and on their Relationship to* Ceratodus Forsteri, *Krefft.* By ALBANY HANCOCK, F.L.S., and THOMAS ATTHEY.

[Plates XIII. & XIV.]

IN our paper on *Ctenodus*, published in the 'Annals' in February 1868*, while recognizing the close connexion between this genus and *Dipterus*, we deemed it prudent to keep the two forms asunder, for certain reasons therein expressed; and the time that has elapsed since then has only tended to confirm us in this opinion. Among other characters that influenced us, stress was laid on the differences in the scales in the two genera; and allusion was made to the fact that the *Dipteri* are all small fishes, and that the *Ctenodi*, on the contrary are, with one exception, all of considerable size.

In the paper alluded to, seven species were described, six of which were new. Three of the seven (namely, *C. cristatus*, *C. tuberculatus*, and *C. corrugatus*) cannot have been less than five or six feet in length. We originally estimated the length at four or five feet; but as larger specimens have since come to hand, we now think that that estimate was too low. Three others (namely, *C. obliquus*, *C. imbricatus*, and *C. ellipticus*) were probably upwards of three feet long. *C. elegans* is quite small. The latter is the only species of which an entire specimen has occurred; and though much crushed and disturbed, its dimensions can be determined with sufficient accuracy: it measures only three inches in length, but, judging from the size of detached dental plates, it probably reaches sometimes nearly twice that length. The *Dipteri* are usually about five or six inches long, and apparently never much exceed that length.

The scales are very different in the two forms. While in *Dipterus* they are circular and truly cycloidal, in *Ctenodus* they (Pl. XIII. fig. 3) are elongated and parallelogrammatic, with the posterior end well rounded, and the sides nearly parallel or a little hollowed or concave; they are in length nearly twice their width, and, though imbricated, can scarcely be called truly cycloidal: they are delicate and large for the size of the fish, and are longitudinally ridged or grooved; the ridges, becoming curved and nodose, form a sort of rosette in the centre of the exposed imbricated portion. This is very different from the ornamentation of the scales of *Dipterus*, which are either irregularly tuberculated, the tubercles being elongated and scattered, or striated and punctate. The scales alone would therefore seem sufficient for generic distinction.

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* "Notes on various Species of *Ctenodus* from the Northumberland Coal-Field," Ann. Nat. Hist. ser. 4. vol. i. p. 77.

There are other characters, however, which distinguish the two forms. When our paper on the subject was written, we had not access to Pander's valuable 'Monograph on the *Ctenodipterini*'[*]. Since then we have enjoyed this advantage, and are now in a position to point out other features that separate *Dipterus* from *Ctenodus*. In the former the upper dental plates are each adherent to the anterior extremities of the two bones named by Pander respectively the palatal and inner pterygoid. These are elongated flattened bones, and lie parallel to and in close contact with each other, being apparently united by a suture. These conjoined bones form on either side of the oral roof a flattened widish plate, with the posterior extremity somewhat expanded. The two plates are united in front along the longitudinal middle line, and diverge widely backwards.

Now the upper dental plates of *Ctenodus* are usually found attached to similar plate-like bones, which incline or diverge to the right or left accordingly as they are united to the right or left dental plate. These bony supports (Pl. XIV. *c*, *d*) are expanded at the posterior extremity, and are in general configuration exactly like the plate composed of the palatal and pterygoid bones in *Dipterus*. Indeed there can be no doubt that they are homologous; but the fact to which we wish to draw attention is, that while in *Ctenodus* the component bones are united so as to form but one bone, the suture being entirely obliterated, they are distinctly separated in *Dipterus* by a well-marked sutural line. This difference would seem to be of some importance; for it appears to be constant, as it occurs in all our species, of the whole of which, excepting *C. corrugatus*, these bones have been found.

The sphenoid bones in the two genera are likewise very different in character. In *Dipterus*, according to the same high authority already quoted, as well as according to Hugh Miller[†], this bone is widely lozenge-formed, and does not extend backwards very much beyond the extremities of the palato-pterygoid bones to which the dental plates are attached, and fills up the entire space between them: this bone Pander considers the basi-sphenoid.

In *Ctenodus* the sphenoid is a much elongated depressed bone, with a wide lozenge-formed expansion near the anterior extremity. In other words, the posterior angle of the lozenge-formed expansion is much produced, while the anterior angle is only slightly produced. The frontal portion (the presphenoid) is rounded, inclining to conical at the extremity, and fits in between the divergent bones that support the dental plates. The lozenge-formed expansion lies partly behind these bones; and the elongated posterior extension (the basisphenoid) is continued for a considerable distance further back, in the large species for nearly five inches. It is therefore pretty clear that in *Dipterus*, in which the sphenoid reaches only a short way behind the extremities of the palatopterygoids, the head is proportionately short in comparison with that of *Ctenodus*, in which it must be much elongated.

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[*] 'Ueber die Ctenodipterinen des Devonischen Systems,' Dr. C. H. Pander. 1858.

[†] See 'Footprints of the Creator,' p. 58.

We have in our possession numerous sphenoids, belonging to five or six species, three of which demonstrably are those of *C. tuberculatus*, *C. obliquus*, and *C. elegans*, respectively. They are all very similar in character, varying only a little in the proportions of the parts. The largest are seven or eight inches long; the smallest, that of *C. elegans*, is only half an inch in length; the usual size is five or six inches. The basisphenoid at its junction with the lozenge-formed expansion is usually thick and nearly circular; elsewhere it is flattened.

In *Dipterus*, too, the vertebræ are ossified; but there is nothing to show that this is the case in *Ctenodus*. Indeed the total absence of any appearance of vertebræ in the specimen of *C. elegans* before referred to is a pretty good proof that in this genus the central axis of the skeleton was cartilaginous.

The above distinctive features will perhaps be considered sufficient to warrant the generic separation of these two forms, notwithstanding their evidently close relationship—and this without referring to the minute structure of the dental plates, which exhibits nevertheless some diversity in character.

In proof of the relationship of the two genera we have only to look to the general form of the oral armature, and to the manner in which the dental plates are placed in the mouth. We have already noticed the similarity of the palato-pterygoid bones to which the upper dental plates are attached, and have pointed out that, while in the one genus the bones are distinct, they are in the other united so that no suture is perceptible. The mandibles (Pl. XIII. fig. 1) are also very much alike in both genera, and so is their relationship to the dental plates.

The cranial bones of *Ctenodus*, so far as we are able to compare them, also closely resemble those of *Dipterus*, in which the whole of them appear to have been determined. Unfortunately, only those of the posterior part of the skull are known in *Ctenodus*. A fragmentary specimen of the occipital region of *C. tuberculatus* in our possession exhibits the occipitals, with a portion of the parietals and the lateral bones, all lying in their natural positions and united into one mass, the component parts being distinguished by well-marked sutures; and the whole so closely resemble the same bones in *Dipterus* that they might be taken to belong to a gigantic specimen of that genus. This fragmentary skull is eight and a half inches across the occiput.

The posterior portions of three other skulls have likewise been found: these belong to *C. obliquus*; they are nearly perfect, and one of them displays the bones up to and including the parietals. The surface is in excellent order, and is more coarsely pitted or punctate than in the former species, and exhibits throughout a semigloss; the sutures are quite distinct. The bones vary in form only specifically from those of *C. tuberculatus*: the occipital is the most characteristic, the frontal margin of which is deeply concave, while in the latter it projects and has a wedge-shaped process in the centre. This beautiful specimen measures seven inches across. The two other examples agree in all their characters with the above; but some of the lateral bones of one side are wanting. As in *Dipterus*, the component bones in *Ctenodus* are comparatively small, vary little in size, are many-sided, and fit together like a mosaic pavement or like the pieces of a Chinese puzzle. And that the anterior bones of the skull are of the same character, we have ample evidence in numerous separate bones that have occurred at Newsham, which, though differing in form from those composing the fragmentary skulls, undoubtedly belong to *Ctenodus*.

Another specimen, showing half of the bones of the occipital region, including the parietals, has occurred. This may perhaps belong to *C. cristatus*; at all events it is a portion of the skull of one of the larger species, for it is of considerable size. And that it cannot belong to either of the above two species is proved by the form of the median occipital, which differs greatly from that of both. It is strongly pointed in front, and the lateral posterior margins are remarkably sinuous; the surface-structure, too, is different.

The bones that are determinable in the above fragmentary skulls are the median and external occipitals, the anterior occipitals, the parietals, and the lateral or "skin bones" according to Pander, of which only the three posterior are present. The arrangement of these bones is precisely similar to that given in Pander's restored figure of the cranial shield of *Dipterus* (tab. 3. fig. 1), the principal difference being that they vary even less in size than those in the figure; the median occipital in *C. tuberculatus* is scarcely, if at all, larger than the other bones. And the surface of the whole, which is in a good state, is devoid of ornamentation, save that it is minutely and irregularly granular and punctate; but the species vary a little in these respects.

In Mr. Atthey's collection of separate cranial bones there are, besides specimens of the above, the median occipital of three or four other species, all varying a little in contour and in surface-character; so that we have here additional corroborative evidence that our shales contain six or seven species of *Ctenodus*.

The opercula likewise resemble those of *Dipterus*; they are large, stout, slightly convex, irregularly circular plates, with one side of the margin a little flattened, and slightly produced at each end of the flattened space; the surface is punctate and granular like the cranial bones. We possess six or seven different forms of these gill-covers, two of which have been identified as belonging to *C. elegans* and *C. obliquus* respectively. But, for a particular description of the various opercula, we must refer to our paper in the 'Annals' previously quoted, merely observing here that the largest are upwards of six inches in diameter; the smallest, that of *C. elegans*, about five sixteenths of an inch, though detached specimens of this species measure as much as nine sixteenths of an inch; all the others are very much larger than this.

The ribs are well ossified both in *Dipterus* and *Ctenodus*. Those of the latter are frequently found associated with other remains of this fish, many of them having been identified with the various species; they are well arched towards the proximal extremity, which is considerably enlarged; and the central channel is quite small, the cylindrical wall of bone being very thick; the ossification of the ribs is, in fact, almost complete. The largest ribs are from six to eight inches long.

The fins, so far as they can be made out in *C. elegans*, are arranged in the same manner as in *Dipterus*. The tail-fin is heterocercal and rhomboidal; and the anal and ventral can be traced, immediately before the caudal.

On the whole, then, it appears quite certain that these two genera are very closely related, as generally considered; but at the same time the several differences already pointed out would seem quite sufficient to justify their generic separation, at least for the present.

We may remark here that a peculiar hatchet-shaped or wedge-formed bone belonging to *Ctenodus* has occurred, which, though we are not able to determine the fact, we believe to belong to the shoulder-girdle*. Several specimens have been found, which are divisible into five or six species by the modification in the form; they are paired bones. Their general character is that of a flattened elongated bone, with one end a little expanded, arched slightly, and gradually thinned out to a fine edge; it narrows a little towards the other end: one of the lateral margins is slightly thickened, and is somewhat convex; the opposite margin is a little concave. From the narrow extremity a strong wide process is given off at right angles, and extends considerably beyond the concave margin.

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* In *Lepidosiren* the shoulder-girdle seems to be reduced to a single large bone having considerable resemblance to the above.

These bones vary a good deal in size and form: some are comparatively narrow and much elongated; others are short and broad; but all have the right-angular process at the narrow extremity. The largest are 4⅝ inches, and the smallest ⅝ inch in length.

These hatchet-shaped bones undoubtedly belong to *Ctenodus*, as they frequently occur with the remains of that fish; and a right and a left specimen have been found in connexion with a crushed head of *C. obliquus*, which fine cranial example exhibits three of the dental plates, both opercula, the sphenoid, the occipitals, and several other bones of the head. No jugular plates have been found; but as they are present in *Dipterus*, they may be expected to occur in *Ctenodus*.

The Hon. William Forster's most interesting discovery of the extraordinary fish which Mr. Gerard Krefft has described under the name of *Ceratodus Forsteri*, will, no doubt, in due course throw a flood of light on these curious Devonian and Carboniferous genera, with which it evidently has much in common. Its relationship to *Ceratodus*, however, is perhaps doubtful. From Mr. Krefft's description*, it appears that in *Ceratodus Forsteri* the skeleton is only partially ossified, in this respect agreeing with *Dipterus* and *Ctenodus*; but from what is known of *Ceratodus*, the latter is probably a true cartilaginous fish, and consequently a Selachian or Placoid. If this were not the case, surely something more would be known of it than the mere dental plates, which do not seem to be uncommon, but which are never found, so far as we know, in connexion with bony supports, with palatal or mandibular bones. In *Ctenodus*, on the contrary, which has the palatal bones and mandible ossified, the dental plates usually occur attached to them. Mr. Atthey has in his collection numerous specimens of the dental plates adhering to entire rami and perfect palato-pterygoid bones. Specimens of all the species, excepting *C. corrugatus*, occur in this state; and, in fact, some portion of the bony support is almost always present. The entire absence, then, in *Ceratodus* of any such bony support would seem to indicate that none had ever existed.

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* Proc. Zool. Soc. 1870, part 2, p. 221.

So long as *Ctenodus* and *Dipterus* were represented merely by the dental plates, they were placed with the Placoids; and no one would have been justified in placing them elsewhere. Therefore, until some further information is obtained respecting *Ceratodus*, it would seem best to allow it to remain as at present located, along with the Selachians. The form of its dental plates, too, is sufficiently characteristic to justify its separation generically from this interesting Australian animal as well as from *Dipterus* and *Ctenodus*. Certainly in the dental organs all three approximate to the Selachians; but the Ganoid characters so predominate that we apprehend no naturalist would hesitate to place them in that order, though they may be considered to a certain extent "synthetic" forms, as suggested by M. Agassiz*.

In the present state of knowledge respecting *Ceratodus*, it is, then, evidently hazardous to place Mr. Krefft's fish in that genus; but its affinity with *Dipterus* and *Ctenodus*, more especially with the latter, is clear enough. All three are covered with large cycloidal scales; the fins are arranged much in the same manner; the skeletons are nearly in the like state of partial ossification; the dental plates are much alike, there being four ridged plates—two palatal, two mandibular. And when the so-called *Ceratodus Forsteri* has been fully examined, there can be little doubt that this affinity will become only the more evident.

Nevertheless the relationship is perhaps closest with *Ctenodus*. Like most of the members of that genus, the Australian fish is large, measuring from three to six feet in length. And it is only necessary to look to the mandibles (Pl. XIII. figs. 1 & 2) of the two forms to be convinced how close this relationship is. In *Ctenodus* the ramus (fig. 2) is a stoutish bone, flattened vertically, with the upper margin turned over towards the external surface, to give support to the large dental plate; it is therefore channelled on the outer surface, and somewhat convex on the inner. The posterior extremity projects backwards beyond the dental plate a little more than half the length of the latter; and is for the greater part occupied by the glenoid surface, which extends from the upper margin, and is a deep, wide, circular notch, inclining backwards and downwards. In front the symphysial surface is straight, extending the whole depth of the ramus, and is grooved transversely. The dental plate is about two-thirds the entire length of the ramus, and is placed nearer the symphysis than the posterior extremity. The ramus is upwards of three inches in length, and, including the thickness of the dental plate, is an inch deep.

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* 'Nature,' No. 61, vol. iii. p. 166 (1870).

Such is the description of the ramus of *C. obliquus*, which, with very little modification, would do equally well for all the other species, as they vary only in size and slightly in the proportions of the parts. On comparing this description and the figure of the ramus (Pl. XIII. fig. 2), as well as that of the entire mandible of *C. imbricatus* (fig. 1), with the representation of the mandible of the so-called *Ceratodus Forsteri* that accompanies the paper on the subject in the 'Proceedings of the Zoological Society,' previously quoted, it will at once be seen that these parts in this curious fish and those in *Ctenodus* closely resemble each other. So similar, indeed, are they, particularly in the dentition, that, were nothing more known of the two forms, they would both assuredly be considered to belong to one and the same genus.

And this likeness would be still greater if the cartilage were present that undoubtedly originally supplemented the ramus of *Ctenodus*. At present the outer border of the dental plate is unsupported, overhanging as it does the side of the ramus. This channel or cavity (Pl. XIII. fig. 2, *d*) beneath the dental plate must have been occupied by cartilage, which, passing backward to the glenoid notch, might, it can easily be seen, form here a semicircular cavity similar to that shown in the figure of the mandible of *Ceratodus Forsteri*. The ramus would thus assume a somewhat rotund form, instead of being a flattened or, rather, a semicylindrical plate, as it has all the appearance of having been, encasing incompletely a cartilaginous core.

But, notwithstanding the similarity of the so-called *Ceratodus Forsteri* to the *Ctenodipterini*, we are quite inclined to believe that it will be found to be generically distinct from all known forms.

The new Australian fish is described to have two "incisor" teeth in the upper jaw, placed a little in advance of the dental plates. There is no reason for believing that such additional teeth are present in either *Dipterus* or *Ctenodus*. Several entire heads of the former have been obtained; and we possess in the specimen before alluded to of *C. elegans* a crushed head of that species, and have also two crushed heads of *C. obliquus*; and in neither genus has there been found the least trace of any such "incisor" teeth. The four dental plates only are present—two palatal, two mandibular. And, again, these plates are not by any means uncommon at Newsham, where upwards of four hundred specimens have been obtained by Mr. Atthey. Had such "incisors" existed, about two hundred of them might therefore have been expected to occur; not one has been found.

This peculiar character alone would seem sufficient to separate generically the so-called *Ceratodus Forsteri* from *Dipterus* and *Ctenodus*, and shows very clearly the relationship of the former to *Lepidosiren*, which is provided with two small pointed teeth in front of the upper dental plates*, which latter do not differ much from those of this interesting Australian fish.

EXPLANATION OF THE PLATES.

PLATE XIII.

Fig. 1. Mandible, natural size, with the dental plate attached, of *Ctenodus imbricatus*: *a*, dental plate; *b*, glenoid notch.

Fig. 2. Outside view, natural size, of the right ramus, with the dental plate attached, of *Ctenodus obliquus*: *a*, dental plate; *b*, symphysial margin; *c*, glenoid notch; *d*, channel or cavity overhung by the dental plate.

Fig. 3. Scale, much enlarged, of *Ctenodus elegans*: *a*, posterior or imbricated extremity.

PLATE XIV.

The palato-pterygoid bones, natural size, with dental plate attached, of *Ctenodus tuberculatus*: *a*, anterior extremity of the bone; *b*, dental plate; *c*, palatal side of the bone; *d*, pterygoid side of ditto.

XXIV.—*Catalogue of* Zygopinæ, *a Subfamily of* Curculionidæ, *found by* Mr. Wallace *in the Eastern Archipelago.* By FRANCIS P. PASCOE, F.L.S. &c., late Pres. Ent. Soc.

[Plates XV. & XVI.]

FOR the Zygopinæ of America and of the Old World Lacordaire sought to establish two sections depending on the, as a rule, greater breadth of the episterna of the metathorax in the former, and their narrowness in the latter, or, when in the latter the episterna are broad, on there being a funicle of only six joints, and the pectoral canal being absent. But, even with these limitations, the distinction will not now hold good, as several genera have broad episterna, either with a pectoral canal or with a seven-jointed funicle.

Lacordaire, however, was acquainted with but three of these Malasian genera, only one of which (*Arachnopus*) has narrow episterna; and this, with *Sphadasmus*, *Sympiezopus*, and their allies, it seems to me, had better be excluded from the subfamily. It is not at present my intention to swerve from Lacordaire's arrangement; still it may be desirable to show how the New-World Zygopinæ may be differentiated from the

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* "Description of the *Lepidosiren annectens*," by Richard Owen, Esq. Trans. Linn. Soc. vol. xviii. p. 341, tab. 27. fig. 2.